Predicting invasion in grassland ecosystems: is exotic dominance the real embarrassment of richness?

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"it is not only winds, currents, and birds that aid the migration of plants; man primarily takes care of this" (von Humboldt, 1805).

Abstract

Invasions have increased the size of regional species pools, but are typically assumed to reduce native diversity. However, global-scale tests of this assumption have been elusive because of the focus on exotic species richness, rather than relative abundance. This is problematic because low invader richness can indicate invasion resistance by the native community or, alternatively, dominance by a single exotic species. Here, we used a globally-replicated study to quantify relationships between exotic richness and abundance in grass-dominated ecosystems in 13 countries on six continents, ranging from salt marshes to alpine tundra. We tested effects of human land use, native community diversity, herbivore pressure, and nutrient limitation on exotic plant dominance. Despite its widespread use, exotic richness was a poor proxy for exotic dominance at low exotic richness, because sites that contained few exotic species ranged from relatively pristine (low exotic richness and cover) to almost completely exotic-dominated (low exotic richness but high exotic cover). Both exotic cover and richness were predicted by native plant diversity (native grass richness) and land use (distance to cultivation). Although climate was important for predicting both exotic cover and richness, climatic factors predicting cover (precipitation variability) differed from those predicting richness (maximum temperature and temperature in the wettest quarter). Herbivory and nutrient limitation did not predict exotic richness or cover. Exotic dominance varied most among regions (subcontinents), whereas cover was greatest in areas with low native grass richness at the site- or regional-scale. Although this could reflect native grass displacement, a lack of biotic resistance is a more likely explanation, given that grasses comprise the most aggressive invaders. These findings underscore the need to

move beyond richness as a surrogate for the extent of invasion, because this metric confounds mono-dominance with invasion resistance. Monitoring species' relative abundance will more rapidly advance our understanding of invasions.

Introduction

Human commerce and migration have breached biogeographic barriers, initiating an unprecedented period of global species migration and homogenization that has intrigued biologists for over 200 years (Candolle & Sprengel, 1821, Darwin, 1859, Elton, 1958, Levine & D'Antonio, 2003, Mack, 2003, Mooney & Cleland, 2001, Qian & Ricklefs, 2006, von Humboldt, 1805). Introduced species currently comprise 20% of some continental floras and 60-80% of some island floras (Vitousek *et al.*, 1997). Invasions can alter basic ecosystem processes, such as water and nutrient cycling, fire frequency, and sediment transport (Levine *et al.*, 2003, Lodge, 1993, Mills *et al.*, 1994, Seabloom & Wiedemann, 1994, Vitousek *et al.*, 1997, Vitousek, 1990), and the associated losses in ecosystem goods and services have been valued at almost 120 billion dollars per year in the USA alone (Pimentel *et al.*, 2005). While exotic species dominate some ecosystems, other ecosystems remain dominated by native species (Candolle & Sprengel, 1821, Darwin, 1859, Elton, 1958, Mack, 1989, von Humboldt, 1805), raising a broadly relevant ecological question: why do exotic plants dominate some locations while other locations remain largely pristine? Centuries after it was posed, this question remains unresolved largely due to a lack of comprehensive, standardized data collected globally across a diversity of community types.

The distribution of invasions may reflect the historical contingencies of evolution, or it may arise deterministically. For example, species that evolved on large and species-rich continents may be inherently competitively superior (Darwin, 1859, Sax & Brown, 2000, van Kleunen *et al.*, 2011), and recent work has shown that a single suite of European species dominates many invaded grasslands worldwide (Firn *et al.*, 2011). Conversely, some ecosystems may be particularly vulnerable to invasion, such as those with low diversity or high levels of disturbance, grazing, introduction of exotic species, or human activity (Crawley, 1987, Davis *et al.*, 2000, Melbourne *et al.*, 2007, Rejmanek, 2003, Sax & Brown, 2000, Seabloom *et al.*, 2006, Shea & Chesson, 2002).

Selection during the invasion process also may create strong biases in exotic species' traits that give the exotics a preferential advantage in certain environments (Gonzalez *et al.*, 2010, Seabloom *et al.*, 2006, van Kleunen *et al.*, 2011). For example, species that are well adapted to human-dominated landscapes are more likely to be introduced by human colonists either intentionally (e.g., domestic plants and animals) or unintentionally (e.g., weeds, pests, and pathogens) (Candolle & Sprengel, 1821, Mack, 1989, Mack, 2003, Sax & Brown, 2000, von Humboldt, 1805) and thus may become invasive when introduced into human-dominated landscapes with high nutrient supply rates, grazing, or disturbance (Antonelli *et al.*, 2011, Davis *et al.*, 2000, Gonzalez *et al.*, 2010, Mack, 1989, Parker *et al.*, 2006, Seabloom *et al.*, 2009). To the degree that invasions arise as a result of human alteration of an ecosystem, the success of species invasions may be more driven by a species ability to exploit human dominated landscapes as opposed to the direct effect of a species' provenance.

Syntheses and meta-analyses have found that exotic richness is often higher in fertile areas where human population, economic activity, habitat conversion, and species introduction rates are the highest (Balmford *et al.*, 2001, Fridley *et al.*, 2007, Rejmanek, 2003, Sax *et al.*, 2002, Scott *et al.*, 2001, Seabloom *et al.*, 2006, Taylor & Irwin, 2004, Williams *et al.*, 2005). However, we currently have little understanding of the patterns of exotic dominance, even though it is likely to be functionally more significant than richness (Levine *et al.*, 2003, Lodge, 1993, Mills *et al.*, 1994, Parker *et al.*, 1999, Seabloom & Wiedemann, 1994, Vitousek *et al.*, 1997), because dominant species have the highest impact on essential ecosystem functions such as primary productivity (Grime, 1998, Hurlbert, 1997). This focus on exotic richness is driven mostly by data availability rather than conservation priorities that often recognize the importance of exotic abundance (Catford *et al.*, 2012).

Many exotic species are relatively benign and their establishment may result in a net increase in diversity with negligible impacts on the native community (Davis, 2003, Firn *et al.*, 2011, Sax *et al.*, 2002). In contrast, notorious invaders (e.g, spotted knapweed, purple loosestrife, and kudzu) may occur in nearly monospecific stands, and the highest dominance of exotics can occur at sites with low exotic diversity due to the presence of one or two highly aggressive species (Catford *et al.*, 2012). Thus, although it is often used as a proxy (e.g., Seabloom *et al.*, 2006, Vitousek *et al.*, 1997), we hypothesize that exotic richness is a highly inconsistent predictor of exotic dominance. Furthermore, we expect a nonlinear relationship, as exotic richness is bounded at 0 species, and relative exotic cover (exotic cover divided by total cover) is bounded between 0 and 100%.

We focus on herbaceous-dominated ecosystems (e.g., grasslands, steppes, old fields, and pastures), because they are globally distributed and play a key role in the biosphere. Grasslands account for about 35% of the Earth's ice-free land mass and net primary production (Chapin *et al.*, 2002, Conant, 2010). With widespread conversion for multiple anthropogenic uses, including 70% of global agriculture, grasslands rank among the most critically endangered biomes (Henwood, 2010, Hoekstra *et al.*, 2005, Ramankutty *et al.*, 2008). Grasslands provide an opportunity to examine fundamental processes that underlie global patterns of invasion. Within the span of the last two centuries, exotic species have overtaken vast expanses of grasslands in Australia, South America, and parts of North America (Firn *et al.*, 2011, Mack, 1989, Mack & Thompson, 1982). In contrast, other areas have apparently remained resistant to invasion (e.g., southern Africa and the central North American Great Plains) (Mack & Thompson, 1982).

We start by examining the relationship between exotic species establishment (exotic richness) and dominance (exotic cover) and test whether exotic richness, a measure widely used in global analyses of exotic invasion (Catford *et al.*, 2012, Fridley *et al.*, 2004), is a reasonable surrogate for exotic dominance. We then quantify variability in exotic cover that is associated with biogeographic regions (i.e., subcontinents) and ecosystem types (e.g., annual grasslands, mesic grasslands, or alpine tundra). We then test whether this variability is associated with the following factors that have been hypothesized or demonstrated to mediate the establishment or dominance of exotic species: **1. human land use** (e.g., agricultural history and proximity to roads, towns, and rivers)(Gelbard & Harrison, 2003, Rejmanek, 2003, Seabloom *et al.*, 2006), **2. environmental gradients** (e.g., precipitation, elevation, and aboveground biomass) (Balmford *et al.*, 2001, Seabloom *et al.*, 2006, Williams *et al.*, 2005), **3. diversity or composition of the native flora** (e.g., total diversity and diversity of key species groups) (Fargione *et al.*, 2003, Fridley *et al.*, 2007, Stohlgren *et al.*, 2003), **4. herbivore pressure** (change in biomass in response to excluding vertebrate herbivores)(Mack, 1989, Parker *et al.*, 2006, Seabloom *et al.*, 2005, Seabloom *et al.*, 2009), and **4. nutrient limitation** (change in biomass in response to fertilization) (Davis *et al.*, 2000, Huenneke *et al.*, 1990, Seabloom, 2007). We use the results of experimental nutrient additions and fencing treatments to directly assess nutrient limitation and herbivore pressure.

Materials and methods

Study System

This work is conducted within the context of the Nutrient Network (NutNet), a globally replicated study of grassland ecosystems. The data in this study are collected from 62 sites located in 13 countries (Argentina, Australia, Canada, China, Estonia, Germany, India, Portugal, South Africa, Switzerland, Tanzania, United Kingdom, USA) on 6 continents (Australia [N = 7], Africa [N=4], Asia [N=2], Europe [N = 9], North America [N = 39], South America [N = 1]; Figure 1, Table A1). We had the highest replication in North America, and these sites also had a large degree of variation in their degree of invasion. We account for within-continent variability with a regional categorical variable nested within continent. Specifically, we divided the North American sites into four regions based on longitudinal mountain ranges (Sierras/Cascades, Rockies, and Appalachians): Pacific Coast, Intermountain West, Central, and Atlantic Coast. These regions broadly correspond with the regions of temperate grasslands and invasions used by Mack (1989) and the biomes used by Olson et al. (2001).

Sites were selected without respect to the dominance of native or exotic species. All sites are dominated by herbaceous species and represent a wide range of ecosystem types including alpine tundra, annual grasslands, mesic grasslands, montane meadows, old fields, salt marshes, savanna, semi-arid grasslands, shortgrass prairie, shrub steppes, and tallgrass prairie. Sites span wide ranges of elevation (0 to 4241 m), mean annual precipitation (211 to 2072 mm yr^{-1}), mean annual temperature (0.3 to 23.7 C), latitude (38 degrees S to 59 degrees N), and aboveground productivity (26 to 1408 g m^{-2} yr^{-1}).

The lead scientist at each site provided latitude and elevation data, and climate data for each site were derived from the WorldClim database (version 1.4; http://www.worldclim.org/bioclim) (Hijmans *et al.*, 2005). In our models we used the following climate variables (BIO designator indicates the variable code in the WorldClim database): mean annual temperature (degrees C; BIO1), mean maximum temperature of the warmest month (BIO5), mean minimum temperature of the warmest month (BIO5), mean annual precipitation (mm per year; BIO12), precipitation seasonality (coefficient of variation in precipitation among months; BIO15), temperature seasonality (standard deviation of temperature among months; BIO4), mean temperature in the wettest quarter (degrees C; BIO8). This suite of climate variable summarizes the mean and seasonality of temperature and precipitation and the seasonal synchrony of rainfall and temperature (i.e., does most of the rain fall during hot or cool times of the year?).

In addition, each scientist provided detailed data on the agricultural history of each site. Here we included two variables summarizing the cultivation and grazing history of each site. To do this, we created an ordered variable summarizing the time since each site had been grazed by domestic livestock: (0) Never grazed, (1) 30 or more years since grazing, (2) 10 to 29 years since grazing, (3) 1 to 9 years since grazing, and (4) Currently grazed. We constructed a similar metric for cultivation with the following categories: (0) Never cultivated, (1) 30 or more years since cultivation, and (2) less than 30 years since cultivation. We used aerial photos of each site (maps.google.com) to assess geographic features associated with invasion including distance to the nearest road, coast, and river, and cultivated land as well as the population of the nearest town or city. Proximity to coastlines, rivers, roads, agricultural land, and human populations centers have all been associated with species invasions (Forman & Alexander, 1998, Mikkelson *et al.*, 2007, Rejmanek, 2003, Seabloom *et al.*, 2006, Small & Cohen, 2004, Taylor & Irwin, 2004).

An observational study was conducted at all sites prior to the start of the experimental treatments. Most sites (N=40) were sampled in three replicate blocks each composed of ten 5×5 m plots for a total of 30 plots per site. Note that at some sites, replication varied: 10 sites had less than 30 plots (range of 10 to 27 plots per site) and 10 sites had more than 30 plots (range of 31 to 60 plots per site). The total data set was composed of 1,889 individual observations including variable replication at some sites. While most sites collected data in 2007 (N=39), data from additional sites were collected in 2008 (N=10), 2009 (N=3), 2010 (N=3), 2011 (N=2), 2012 (N=3), 2013 (N=2).

At a subset of the sites (N=39), we conducted a replicated experiment that allowed us to estimate herbivore pressure and nutrient limitation. The experiment was a full factorial combination of nutrient addition (Control or Fertilized) and consumer density (Control or Fenced) for a total of 4 treatments. Fences were 2.1 m tall, and designed to exclude large aboveground mammalian herbivores, including ungulates. The first 90 cm was 1 cm woven wire mesh with a 30 cm outward-facing flange stapled to the ground to exclude digging animals; climbing and subterranean animals potentially could access plots. Nutrient addition rates and sources were: 10 g N m^{-2} yr^{-1} as timed-release urea, 10 g P m^{-2} yr^{-1} as triple-super phosphate, 10 g K m^{-2} yr^{-1} as potassium sulfate and 100 g m^{-2} yr^{-1} of a micronutrient mix (6% Ca, 3% Mg, 12% S, 0.1% B, 1% Cu, 17% Fe, 2.5% Mn, 0.05% Mo, and 1% Zn). N, P, and K were applied annually; the micronutrient mix was applied once at the start of the study to avoid toxicity of largely immobile micronutrients.

Ammonium nitrate was used as the nitrogen source in 2007, however urea was used in all subsequent years due to difficulties in procuring ammonium nitrate. We tested whether various nitrogen sources could alter community responses by conducting an experiment comparing the two nitrogen sources (timed-release urea, and ammonium nitrate) at four NutNet sites (Bunchgrass, Hopland, Lookout, and Mclaughlin; Table A1). At each site, we established a fully randomized complete block design with 3 treatments (Control and 10 g of N added as either timed-release urea or ammonium nitrate) and 3 blocks (9 plots per site and 36 plots total). Each plot was 2 x 2 m. We applied the treatments in spring 2009 and sampled the cover and biomass of the plots in 2010 as described below. We found no difference in richness or total live biomass among the nitrogen sources based on a mixed effects model with site and block within site treated as random effects (p = 0.374 for biomass and p=1.000 for richness).

Sampling. Areal cover of all species was estimated visually to the nearest 1% in a 1m^2 quadrat in each 5 × 5 m plot. Typically there were 30 cover plots per site. Cover was estimated independently for each species so that total summed cover exceeded 100% for multilayer canopies. At some sites with strongly seasonal communities, cover was estimated twice during the year and the maximum cover of each species was used in the analyses. Lead scientists at each site provided the provenance of each species that occurred at their sites. Across the study sites, some species occurred in both their native and exotic range (Firn *et al.*, 2011). Aboveground biomass was collected in two 10 × 100 cm strips (0.2 m^2 in each plot) clipped at peak biomass in each 5 × 5-m plot for an average 30 biomass samples per site. Biomass was sorted to functional group (i.e. grass, forb, legume, bryophyte, litter), and the current year's production was dried to constant mass at 60°C, and weighed to the nearest 0.01 g.

Statistical Analyses. All analyses were conducted using R version 2.15 (R Development Core Team, 2010). We examined the relationship between exotic richness and cover and the following bioclimatic drivers: elevation (m), mean annual precipitation (MAP; mm yr^{-1}), seasonal precipitation variability (coefficient of variation in monthly precipitation), mean annual temperature (C), mean minimum annual temperature (C), mean maximum annual temperature (C), seasonal temperature variability (standard deviation in mean monthly temperature), temperature in the wettest quarter (C), aboveground dead biomass (g m^{-2}), and aboveground live biomass (g m^{-2} yr^{-1}). We tested whether the richness of local flora (i.e., cumulative number of species at each site) was correlated with exotic establishment or dominance by including site-level native species richness. We also included the richness of native species of different lifespan (annual or perennial) and lifeform (grasses, forbs, and woody plants). There were insufficient data at one site to fully classify species by lifeform and lifespan, and this sites was not included in regressions including these variables.

We tested whether exotic richness or cover were related to herbivore pressure or nutrient limitation at each of the experimental sites (N=39) after a single year of treatment (Fencing or Fertilization). We calculated the treatment effects after a single year as the best direct measure of the herbivore effects and nutrient limitation independent of compositional changes and species extinctions that become increasingly important after multiple years of treatments. We estimated herbivore pressure as the change in live biomass resulting from fencing calculated as the log ratio $\log(B_{f-}/B_{f+})$, where B_{f-} is the live biomass in control plots and B_{f+} is the live biomass in fenced plots after one year of fencing treatment. We estimated nutrient limitation by calculating the change in live biomass resulting from nutrient addition calculated as the log ratio $\log(B_{nut+}/B_{nut-})$, where B_{nut-} is the live biomass in unfertilized plots and B_{nut+} is the live biomass in fertilized plots after one year of nutrient addition treatments.

We calculated exotic cover as a relative measure by summing cover of all exotic species and dividing by the summed cover of all species. We modeled the cover of exotic species as a proportion ranging from 0 to 1.0 using generalized linear models with logit link and binomial error (i.e., logistic regression), and modeled exotic richness (number of exotic species per m^2) using a log link and Poisson errors (i.e., Poisson regression). All regression models started with the following variables: elevation (log m); precipitation (mm yr^{-1}); seasonal precipitation and temperature variation; mean, maximum, and minimum annual temperature (C); aboveground live biomass (log g m^{-2} yr^{-1}); aboveground dead biomass (log g m^{-2}); richness of native species, native annuals, native grasses, native forbs, native woody plants, herbivore pressure (i.e., fencing effect on biomass); nutrient limitation (fertilization effect on biomass); years since last grazing and cultivation; distance to the nearest road, river, cultivated land, and coast; and the population of the nearest town.

We used quasi-likelihood to adjust for over- or under-dispersion in the data. It is not possible to calculate AIC or similar likelihood based statistics from quasi-likelihood models (Venables & Ripley, 2003), so we reduced the models using backwards selection and Type II sums of squares to include only those variables explaining significant amount of variation using the F statistic. We also conducted the analyses using transformations for the richness (square root) and proportion exotic cover (arcsine square root), and results were qualitatively similar. Finally, we had similar results analyzing the plot-scale data using mixed-effects models with site as a random effects (Pinheiro & Bates, 2000).

We were missing data on live biomass at 4 sites, fencing and fertilization effects on biomass at 23 sites, and cultivation or grazing history at 26 sites. Biomass, fencing effects, fertilization effects, cultivation history, grazing history, and land-use data were not present in any of the of the final statistical models (i.e., the parsimonious models after selection), so we present results of models fit to the larger data set excluding these variables. Results did not differ qualitatively across these different subsets of the data.

Results

Across sites ranging from salt marshes to alpine tundra (Figure 1; Table A1), we documented 1,477 species from 102 families. The 191 exotic species comprised 34 families. We were unable to classify the provenance of 129 taxa due to either taxonomic or provenance uncertainties (9% of the total species). Unclassified species comprised 7% of the cover in the total data set, and we have no reason to expect that unclassified species were biased with regards to their provenance. Relative exotic cover (100*exotic cover/total cover) varied from 0 to 100% at both the plot (n = 1,924) and site scales (n = 62). Exotic richness ranged from 0 to 46 species at the site scale (cumulative exotic richness) and 0 to 20 species at the plot scale (i.e., mean exotic richness m^{-2}). Note that hereafter we only analyze mean exotic richness at the plot scale, as the mean plot scale richness is highly correlated with cumulative exotic richness across all plots at each site ($r = 0.84$, $p < 0.001$).

Exotic cover and exotic richness were positively correlated at the site and plot scale (Figure 2; Table 1), however the relationship was strongly nonlinear. In addition, exotic cover was highly variable at low levels of species richness. For example, while sites with an average of 10 or more exotic species were always dominated by exotic species (> 80% exotic cover), sites with less than 3 exotic species spanned the range from 0 to 96% exotic cover. As a result of the higher variance in exotic cover at sites with low exotic richness, the residuals around the regressions were much larger at low levels exotic richness (Inset Figure 2). Thus, exotic richness provides a lower bound on exotic dominance, but exotic richness does not discern between sites with a few sparse invaders (low exotic richness and cover) and those dominated by a few highly abundant exotic species (low exotic richness but high exotic cover).

Most of the variability in exotic richness and cover at the plot scale was due to differences among regions and ecosystems; there was almost no variability accounted for by differences among continents (Figure 3), as even highly invaded continents had areas dominated by native species (e.g., the Central Great Plains of North America; Figure 1 & 5). Exotic cover varied most strongly among regions (44%). While exotic richness also had significant variation among regions (30% of variance), it varied much more among sites within a single ecosystem in a region (42% of variance). In terms of regional variation in exotic cover, all sites in Africa, Asia, and Europe were dominated by native species, as measured by richness or cover, whereas all sites on the Pacific coast of North America were highly invaded (Figure 4A). Variation among different ecosystems was equally strong. Alpine, montane, salt marsh, and shrub steppe sites had less than 10% exotic cover, whereas annual grasslands had more than 75% exotic cover (Figure 4B).

In part, these differences among regions and ecosystems reflect underlying biotic, climatic, and human land use gradients. Site-level means of exotic cover and richness were lowest in areas with a diverse native grass flora (number of grass species at a site) and at sites located far from cultivated agricultural fields (Table 2). Exotic cover was also higher in areas with consistent precipitation (low variance among months), and exotic richness was higher at hot (high maximum temperature) sites near the coast that have a cool wet-season.

The strong and consistent effects of native grass richness likely reflect the dominance of grasses, as a group. Native grasses comprised the highest percent of native plant cover (mean = 46.9% ± 3.5% SEM). Forbs were the next most abundant group (mean = 35.1% ± 3.3% SEM). In contrast, average forb diversity (mean = 16.9 ± 1.9 SEM species m^{-2}) was higher than grasses (mean = 6.2 ± 0.7 SEM species m^{-2}). The strong negative relationship between native grass richness and exotic species cover also could occur if exotic cover and native grass richness were driven by the same underlying factors. To test this possibility, we compared models of exotic cover and native grass richness that did not use the diversity of the native flora as an explanatory variable. Although both responded to climate, the strength and direction of factors controlling native grass richness were different than those driving exotic cover (Table A2), providing little evidence for a shared latent factor.

The following variables were not included in any of the reduced models: minimum annual temperature (C); aboveground live biomass (log g m^{-2} yr^{-1}); aboveground dead biomass (log g m^{-2}); richness of native species, native annuals, native grasses, native forbs, native woody plants, herbivore pressure (i.e., fencing effect on biomass); nutrient limitation (fertilization effect on biomass); years since last grazing and cultivation; distance to the nearest road, river; and the population of the nearest town. Thus, while native community flora, climate, and land use all influence exotic cover and richness, only a few of these commonly used factors were ever retained in models. Herbivore pressure and nutrient limitation of productivity were never correlated with global measures of exotic richness or cover.

Discussion

Using data from a multi-continent, replicated study, we found exotic richness to be an inconsistent predictor of exotic dominance at sites with low exotic richness. While sites with many exotic species were uniformly exotic dominated, sites with few exotic species could either be largely native or completely dominated by one or two exotic species. In grasslands, much of this variation arose from differences among regions within continents (the Atlantic and Pacific coasts of North America were highly invaded, but the Midwest was not) and ecosystem types (annual grasslands, savannas, pastures, old fields were dominated by exotics). Region and ecosystem type are interrelated. For example, all of the Atlantic coast sites are old fields or savanna and 57% of the Pacific coast sites are annual grasslands or savanna. Human land use, native community diversity, and environmental gradients (i.e., climate) were all correlated with invasion. Specifically, the strongest predictor of exotic richness and cover was the number of native grass species present in the site or regional flora, with more native grass species negatively correlated with exotic grass richness. In addition, exotic richness and cover were both higher at sites that were close to cultivated land. Climate also played a role in determining invasion, however climatic effects were different for exotic and native richness. Exotic cover was highest in sites that had low rainfall seasonality, while exotic richness was highest at sites in hot areas (high maximum temperature) with a pronounced cool and wet season.

Despite the historical and continued focus on exotic richness (Fridley *et al.*, 2007), we found that exotic richness was only an effective predictor of exotic dominance when exotic richness was very high (i.e., greater than 10 exotic species per m^2). Exotic richness could not resolve the difference between two distinct types of sites with low exotic species richness: those sites that are relatively pristine with a few rare exotic species and those that are dominated by a few highly dominant exotic species. Thus, examination of only exotic richness hinders our understanding of drivers of invasion by confounding these qualitatively different site types, both with low exotic richness. The poor predictive capacity of exotic richness suggests the need for efforts like the work presented here that measure exotic dominance in standard and comparable ways across many sites.

The importance of native grass richness as a predictor of exotic cover suggests that evolutionary history may be a critical component in understanding invasions. Interestingly, it is the diversity of grasses and not diversity *per se* that appears to mediate the dominance of exotic species. In addition, we find the strongest relationship between exotic cover and cover of the most abundant group of native plants (i.e. grasses) as opposed to the most diverse (i.e. forbs). Exotic grasses are particularly effective invaders and tend to be more abundant in their invasive range (Firn *et al.*, 2011), and colonization by new species can be impeded by presence of resident species that are functionally similar (Fargione *et al.*, 2003). Regions that have evolved diverse grass floras may be more likely to contain native species that overlap the niches of a particularly effective group of invaders (i.e., grasses), conferring invasion resistance. Ultimately, drawing inferences about diversity-invasibility relationships using observational data requires caution, because of possible covariates that may confound causal native exotic richness relationships (Fridley *et al.*, 2007, Rejmanek, 2003).

Given the wide range of environmental conditions spanned by this work and the diversity of exotic taxa represented across these sites, we did not expect to find consistent environmental drivers of exotic species richness and cover. Nevertheless, we did find that both exotic cover and richness were increased by the propinquity of cultivated lands. In addition, exotic richness was higher in coastal areas. Human endeavors, including agriculture, undoubtedly increase invasion as has been shown in many other studies (Antonelli *et al.*, 2011, Davis *et al.*, 2000, Gelbard & Harrison, 2003, Gonzalez *et al.,* Mack, 1989, Parker *et al.*, 2006, Rejmanek, 2003, Scott *et al.*, 2001, Seabloom *et al.*, 2009, Seabloom *et al.*, 2006, Taylor & Irwin, 2004, Williams *et al.*, 2005).

Studies replicated at the regional, as opposed to the global scale, have found higher exotic richness in low-lying coastal areas (Alexander *et al.*, 2011, Rejmanek, 2003, Seabloom *et al.*, 2006, Williams *et al.*, 2005); however indirect factors like coastal proximity and elevation are often highly correlated with many potential invasion-drivers including native richness, species introduction rates, ecosystem productivity, human population, and conversion of land to human-dominated uses (Balmford *et al.*, 2001, Rejmanek, 2003, Scott *et al.*, 2001, Seabloom *et al.*, 2002, Seabloom *et al.*, 2006, Williams *et al.*, 2005). While we found more exotic species at sites near coastlines, elevation was not included in the best model of exotic dominance or richness.

We did not find a detectable impact of large herbivore pressure on exotic occurrence and dominance. However, other studies have shown that preferential consumption of native plants by herbivores may increase invasions (Orrock *et al.*, 2008, Orrock *et al.*, 2009, Seabloom *et al.*, 2009), although the strength and direction of herbivore effects are contingent upon the amount of shared evolutionary history between herbivores and plants (Mack, 1989, Parker *et al.*, 2006, Verhoeven *et al.*, 2009). At a broader scale, the areas in our study that are highly invaded are concordant with those highlighted by Mack (1989) as possibly lacking an evolutionary history with congregating, hoofed grazers during the Holocene, such as Australia and the Pacific coast of North America. In contrast, sites with high native grass diversity and low cover of exotics have a long history of grazing by hoofed mammals, such as Eurasia, Africa, and the Central Great Plains of North America (Mack, 1989).

While it is clear that biological invasions have altered many of the world's ecosystems and precipitate significant economic costs (Levine *et al.*, 2003, Lodge, 1993, Mills *et al.*, 1994, Pimentel *et al.*, 2005, Seabloom & Wiedemann, 1994, Vitousek *et al.*, 1997, Vitousek, 1990), we still have little ability to make general predictions about which species will have the greatest impacts as invaders and which areas are likely to be the most impacted (Catford *et al.*, 2012, Firn *et al.*, 2011, Parker *et al.*, 1999, Seabloom *et al.*, 2003). The search for general drivers of invasion at the global scale has been hindered by the lack of consistent, globally replicated data on exotic abundance, and a resulting overemphasis on exotic richness as a surrogate for impact. Here we show that exotic richness is only an effective predictor of exotic dominance when richness is exceptionally high; overall, exotic richness represents a poor proxy for the impact, assessed here via exotic cover, of exotic species on native communities. Our global-scale observations bridge the gap between mechanistic studies at single sites and meta-analyses of global patterns of exotic richness, shedding new light on the drivers and outcomes of global invasions.

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Tables

Table 1. Results of logistic regression of exotic cover on exotic richness at the site scale (N=62). Tests of significance are based on quasi-likelihood due to significant under- or over-dispersion in the data. Estimated dispersion parameter was 0.52.

Source	Estimate	S.S.	D.F.	F	p
Exotic Richness	0.5629	26.209	1	50.428	<0.0001
Residuals		31.184	60		

Table 2. Final regression model of exotic cover and exotic richness at the site scale (N=62) explained by environmental covariates. Tests of significance are based on quasi-likelihood due to significant over- or under-dispersion in the data. Only the reduced model is shown. The full model included elevation (m); precipitation (mm yr^{-1}); seasonal precipitation and temperature variation; mean, maximum, and minimum annual temperature (C); aboveground live biomass (log g m^{-2} yr^{-1}); aboveground dead biomass (log g m^{-2}); richness of native species, native annuals, native grasses, native forbs, native woody plants, herbivore pressure (i.e., fencing effect on biomass); nutrient limitation (fertilization effect on biomass); years since last grazing and cultivation; distance to the nearest road, river, cultivated land, and coast; and the population of the nearest town. Estimated dispersion parameter for quasi-likelihood was 0.70 for exotic cover and 2.15 for exotic richness.

Response	**Source**	**Estimate**	**S.S.**	**D.F.**	**F**	**p**
Exotic Cover	Native Grass Richness	-0.362	16.92	1	24.3	0.000
	Precipitation Variation	0.050	6.93	1	10.0	0.003
	Distance to Cultivation	-1.022	3.37	1	4.8	0.032
	Residuals		39.62	57		
Exotic Richness	Native Grass Richness	-0.163	36.93	1	17.2	0.000
	Distance to Coast	-0.511	22.03	1	10.3	0.002
	Maximum Temperature	0.117	20.56	1	9.6	0.003
	Temp. Wettest Quarter	-0.048	9.44	1	4.4	0.041
	Distance to Cultivation	-0.338	9.44	1	4.4	0.041
	Residuals		118.20	55		

Figure Legends

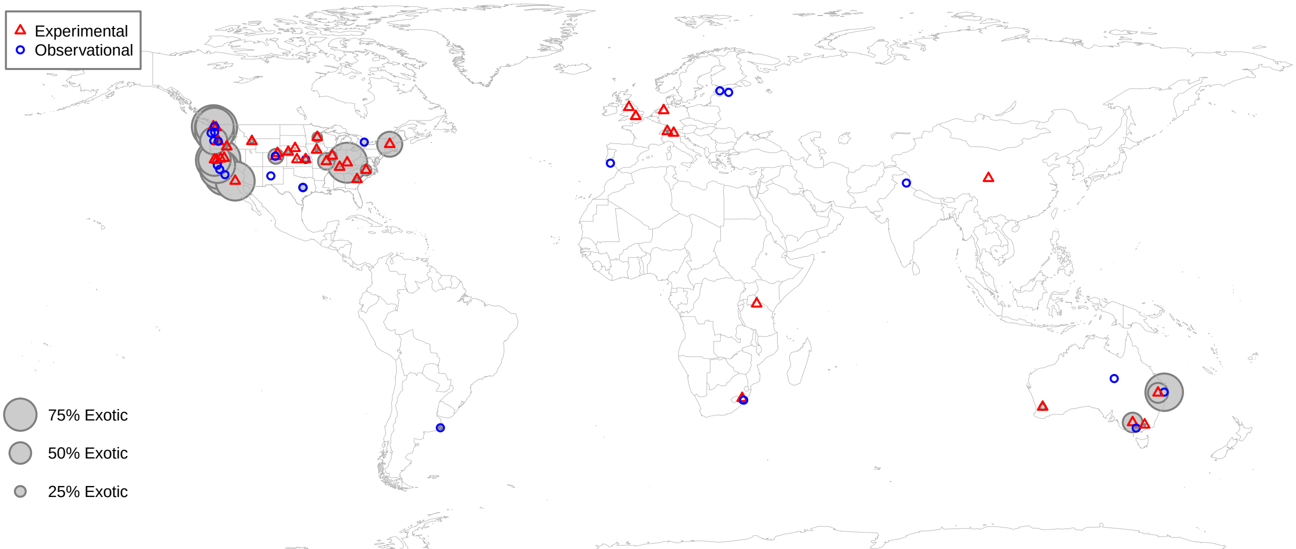
Figure 1. Nutrient Network sites included in the current analyses. Observational sites only have a single year of data and no experimental manipulations. Experimental sites have one year of pre-treatment data in addition to data after the start of the fencing and nutrient-addition treatments. Gray shaded circles are proportional to exotic cover.

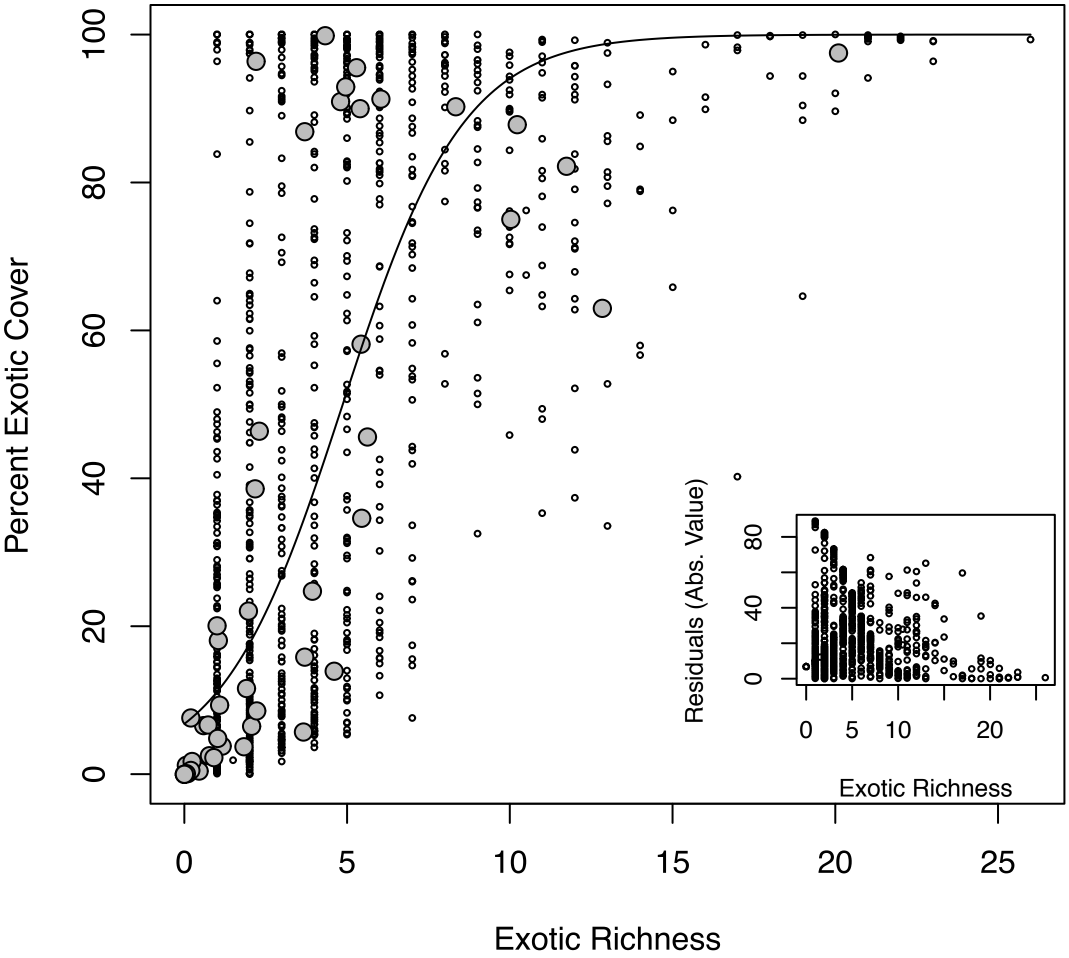
Figure 2: Logistic regression showing relationship between exotic richness and mean cover of exotic species in 1,924 plots in 62 grassland sites in 13 countries. Small open circles are plot-scale data and larger gray circles show site means. Solid line shows predicted relationship based on a logistic regression of the plot-scale data for exotic cover and richness ($F= 49.5$; $p < 0.001$). Inset shows the absolute value of the regression residuals.

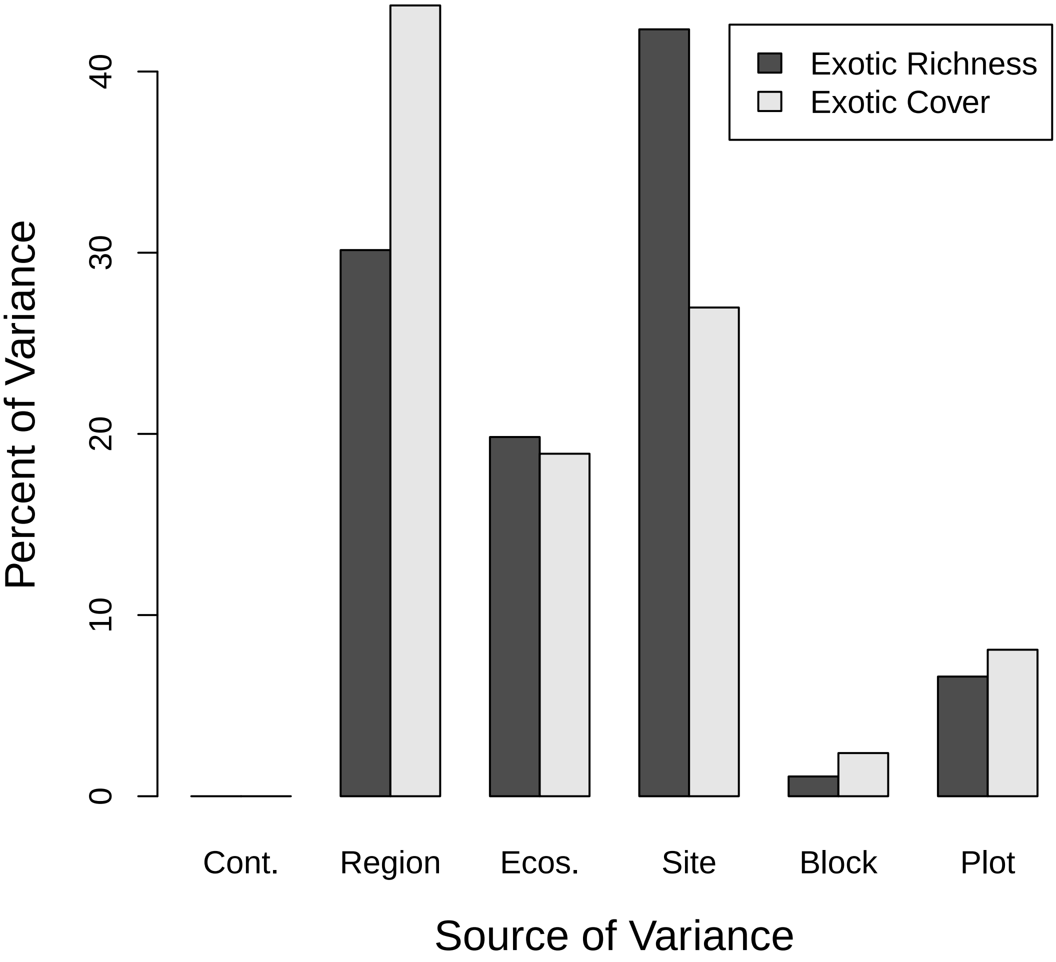
Figure 3: Variance components analysis showing distribution of variance in exotic richness and exotic cover (percent of total) among 1,924 plots sampled at 62 sites in 13 countries. Sources of variation are the following nested terms: continent, region, ecosystem, site, block, and plot (residual) level variation.

Figure 4: Exotic cover (percent of total) by region (A.) and ecosystem (B.) at 62 sites in 13 countries. Pacific-coast, central, intermountain-west, and Atlantic-coast are regions within North America. Error bars are 1 SEM and numbers in parentheses are the number of sites in each category.

Figure 5: Regressions showing relationship between mean cover and richness of exotic species and the total richness of native grass species at 62 grassland sites in 13 countries. Regression lines for percent cover are logistic regressions and for richness are Poisson regressions.


△ Experimental
○ Observational
75% Exotic
50% Exotic
25% Exotic


Percent Exotic Cover
0
20
40
60
80
100
Exotic Richness
0
5
10
15
20
25
Residuals (Abs. Value)
0
40
80
Exotic Richness
0
5
10
20


Exotic Richness
Exotic Cover
Percent of Variance
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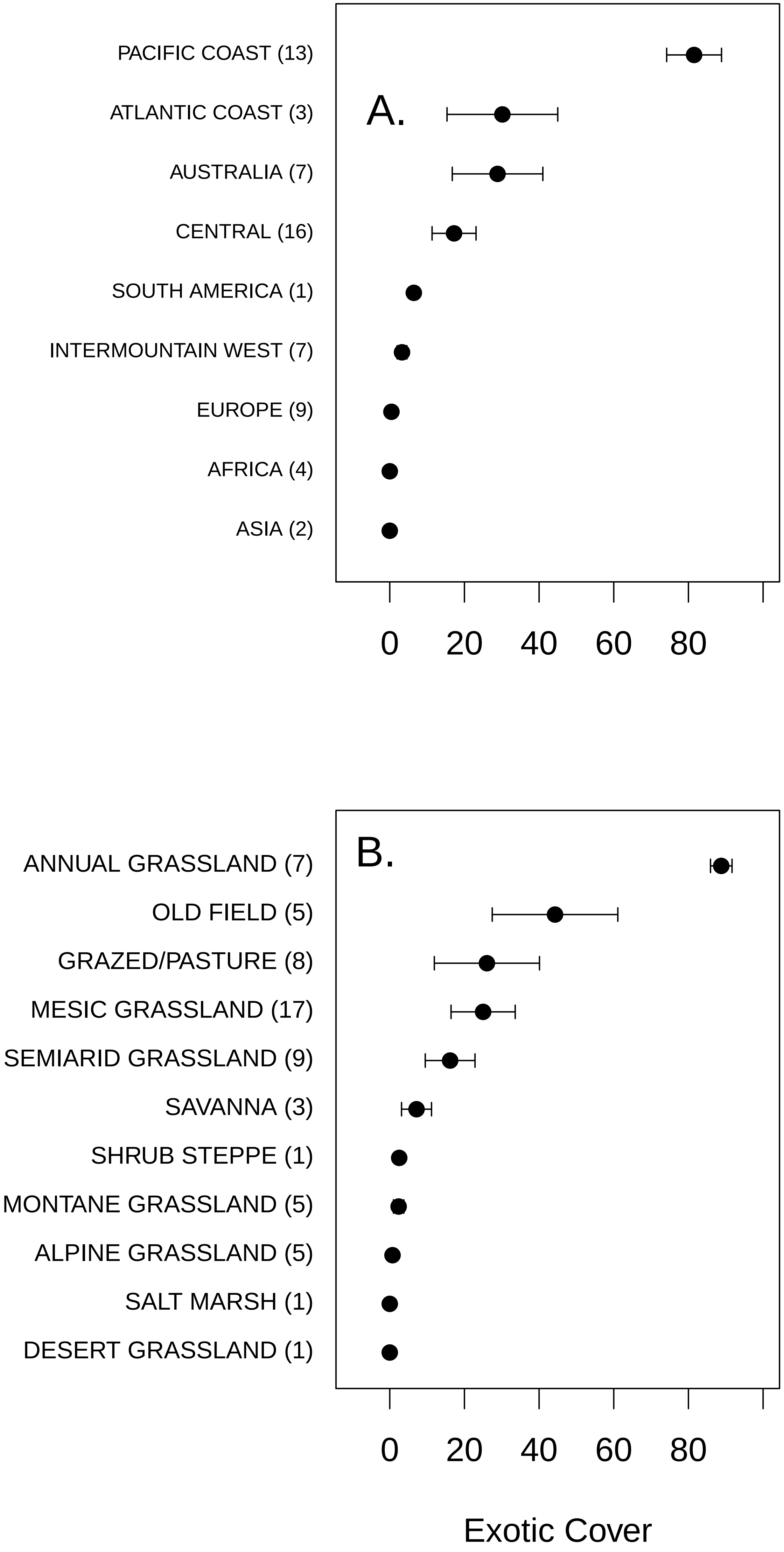
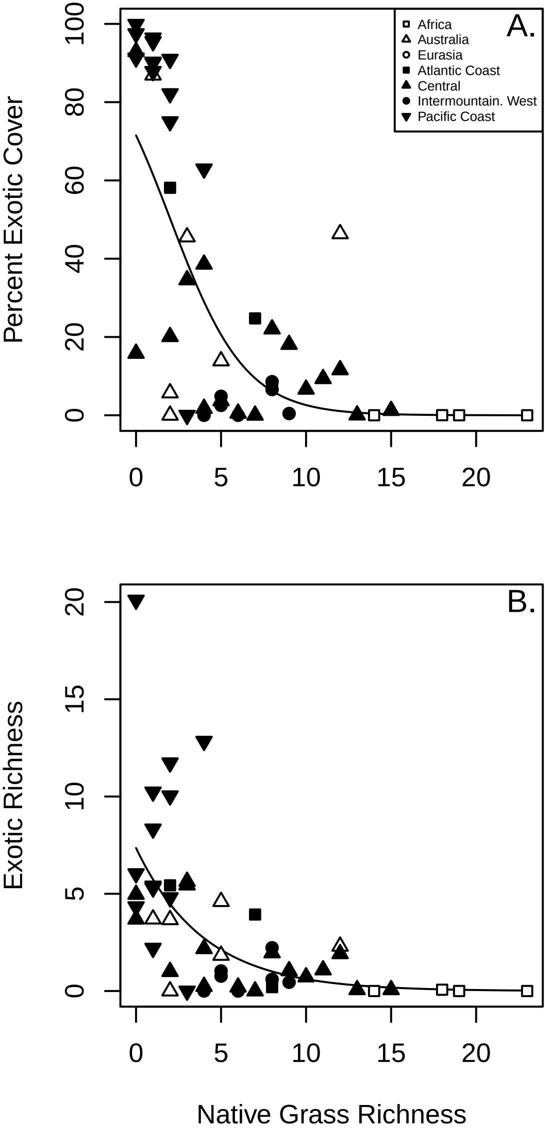
30
40
Cont.
Region
Ecos.
Site
Block
Plot
Source of Variance


A.
PACIFIC COAST (13)
ATLANTIC COAST (3)
AUSTRALIA (7)
CENTRAL (16)
SOUTH AMERICA (1)
INTERMOUNTAIN WEST (7)
EUROPE (9)
AFRICA (4)
ASIA (2)
0
20
40
60
80
B.
ANNUAL GRASSLAND (7)
OLD FIELD (5)
GRAZED/PASTURE (8)
MESIC GRASSLAND (17)
SEMIARID GRASSLAND (9)
SAVANNA (3)
SHRUB STEPPE (1)
MONTANE GRASSLAND (5)
ALPINE GRASSLAND (5)
SALT MARSH (1)
DESERT GRASSLAND (1)
0
20
40
60
80
Exotic Cover


A.
B.
□ Africa
△ Australia
○ Eurasia
■ Atlantic Coast
▲ Central
● Intermountain. West
▼ Pacific Coast
Percent Exotic Cover
0
20
40
60
80
100
Exotic Richness
0
5
10
15
20
0
5
10
15
20
Native Grass Richness

Supplementary Online Appendices

Table A1: Study sites included in analyses. Pretreatment observational data were collected at all sites. Subsequent fertilization and fencing were only conducted at experimental sites. Study type indicates if sites had observation data only (Obs.) or observational and experimental fencing and fertilization data (Exp.).

Site	Name	Continent	Region	Country	Ecosystem	Lat.	Lon.	Elev. (m)	Precip. (mm)	Study Type	Number of Plots	First Sample Year
1	Serengeti	Africa	Africa	Tanzania	Savanna	-2.25	34.51	1536	854	Exp.	30	2008
2	Mt Gilboa	Africa	Africa	South Africa	Montane Grassland	-29.28	30.29	1748	926	Exp.	30	2010
3	Summerveld	Africa	Africa	South Africa	Mesic Grassland	-29.81	30.72	679	939	Obs.	30	2010
4	Ukulinga	Africa	Africa	South Africa	Mesic Grassland	-29.67	30.40	842	880	Obs.	30	2009
5	Azi	Asia	Asia	China	Alpine Grassland	33.67	101.87	3500	667	Exp.	30	2007
6	Kibber (Spiti)	Asia	Asia	India	Alpine Grassland	32.32	78.01	4241	504	Obs.	30	2011
7	Bogong	Australia	Australia	Australia	Alpine Grassland	-36.87	147.25	1760	1592	Exp.	30	2009
8	Burrawan	Australia	Australia	Australia	Semiarid Grassland	-27.73	151.14	425	683	Exp.	30	2008
9	Derrimut	Australia	Australia	Australia	Semiarid Grassland	-37.81	144.79	38	574	Obs.	30	2007
10	Ethabuka (South Site)	Australia	Australia	Australia	Grazed Pasture	-23.64	138.40	104	211	Obs.	28	2013
11	Kinypanial	Australia	Australia	Australia	Semiarid Grassland	-36.20	143.75	90	426	Exp.	30	2007
12	Mt. Caroline	Australia	Australia	Australia	Savanna	-31.78	117.61	285	330	Exp.	40	2008
13	Pinjarra Hills	Australia	Australia	Australia	Grazed Pasture	-27.53	152.92	38	1133	Obs.	30	2013
14	Fruebuel	Europe	Europe	Switzerland	Grazed Pasture	47.11	8.54	995	1355	Exp.	30	2008
15	Val Mustair	Europe	Europe	Switzerland	Alpine Grassland	46.63	10.37	2320	1098	Exp.	30	2008
16	Papenburg	Europe	Europe	Germany	Old Field	53.09	7.47	0	783	Exp.	10	2007
17	Elva	Europe	Europe	Estonia	Semiarid Grassland	58.26	26.35	64	616	Obs.	10	2012
18	Kirikukyla	Europe	Europe	Estonia	Mesic Grassland	58.71	23.80	8	601	Obs.	30	2012
19	Companhia das Lezirias	Europe	Europe	Portugal	Grazed Pasture	38.00	-8.00	200	554	Obs.	31	2012
20	Heronsbrook (Silwood Park)	Europe	Europe	United Kingdom	Mesic Grassland	51.41	-0.64	60	692	Exp.	30	2007
21	Lancaster	Europe	Europe	United Kingdom	Grazed Pasture	53.99	-2.63	180	1322	Exp.	26	2008
22	Rookery (Silwood Park)	Europe	Europe	United Kingdom	Mesic Grassland	51.41	-0.64	60	706	Exp.	30	2007
23	Koffler Scientific Reserve	North America	Central	Canada	Grazed Pasture	44.02	-79.54	301	815	Obs.	36	2010
24	Cowichan	North America	Pacific Coast	Canada	Old Field	48.46	-123.38	50	764	Exp.	30	2007
25	Hanover	North America	Atlantic Coast	USA	Old Field	43.42	-72.14	271	1033	Exp.	30	2007
26	Savannah River	North America	Atlantic Coast	USA	Savanna	33.34	-81.65	71	1194	Exp.	20	2007
27	Duke Forest	North America	Atlantic Coast	USA	Old Field	36.01	-79.02	141	1163	Exp.	30	2007
28	Barta Brothers	North America	Central	USA	Semiarid Grassland	42.24	-99.65	767	597	Exp.	30	2007
29	Boulder South Campus	North America	Central	USA	Semiarid Grassland	39.97	-105.23	1633	425	Exp.	20	2008
30	Chichaqua Bottoms	North America	Central	USA	Mesic Grassland	41.79	-93.39	275	855	Exp.	54	2009
31	Cedar Creek LTER	North America	Central	USA	Mesic Grassland	45.40	-93.20	270	750	Exp.	50	2007
32	Cedar Point Biological Station	North America	Central	USA	Semiarid Grassland	41.20	-101.63	965	445	Exp.	60	2007
33	Hall's Prairie	North America	Central	USA	Mesic Grassland	36.87	-86.70	194	1282	Exp.	30	2007
34	Konza LTER	North America	Central	USA	Mesic Grassland	39.07	-96.58	440	877	Exp.	30	2007
35	KonzaN1B	North America	Central	USA	Mesic Grassland	39.08	-96.56	440	878	Obs.	12	2007

36	Saline Experimental Range	North America	Central	USA	Semiarid Grassland	39.05	-99.10	440	607	Exp.	30	2008
37	Sevilleta LTER	North America	Central	USA	Desert Grassland	34.36	-106.69	1600	252	Obs.	40	2007
38	Shortgrass Steppe LTER	North America	Central	USA	Semiarid Grassland	40.82	-104.77	1650	365	Exp.	30	2007
39	Spindletop	North America	Central	USA	Grazed Pasture	38.14	-84.50	271	1140	Exp.	30	2007
40	Temple	North America	Central	USA	Mesic Grassland	31.04	-97.35	184	871	Obs.	26	2007
41	Trelease	North America	Central	USA	Mesic Grassland	40.08	-88.83	200	982	Exp.	30	2008
42	Tyson	North America	Central	USA	Old Field	38.52	-90.56	169	997	Exp.	40	2007
43	Bunchgrass (Andrews LTER)	North America	Intermountain West	USA	Montane Grassland	44.28	-121.97	1318	1647	Exp.	30	2007
44	Buttercup (Andrews LTER)	North America	Intermountain West	USA	Montane Grassland	44.28	-121.96	1500	1718	Obs.	30	2007
45	Hart Mountain	North America	Intermountain West	USA	Shrub steppe	42.72	-119.50	1508	272	Exp.	30	2007
46	Lookout (Andrews LTER)	North America	Intermountain West	USA	Montane Grassland	44.21	-122.13	1500	1898	Exp.	30	2007
47	Niwot Ridge LTER	North America	Intermountain West	USA	Alpine Grassland	39.99	-105.38	3050	439	Obs.	40	2007
48	Sagehen Creek UCNRS	North America	Intermountain West	USA	Montane Grassland	39.43	-120.24	1920	882	Exp.	30	2007
49	Sheep Experimental Station	North America	Intermountain West	USA	Grazed Pasture	44.24	-112.20	910	262	Exp.	40	2007
50	American Camp	North America	Pacific Coast	USA	Mesic Grassland	48.47	-123.01	41	557	Obs.	30	2007
51	Elliott Chaparral	North America	Pacific Coast	USA	Annual Grassland	32.88	-117.05	200	331	Exp.	30	2008
52	Finley NWR	North America	Pacific Coast	USA	Mesic Grassland	44.41	-123.28	68	1104	Obs.	19	2007
53	Glacial Heritage	North America	Pacific Coast	USA	Mesic Grassland	46.87	-123.03	33	1311	Obs.	30	2007
54	Hastings UCNRS	North America	Pacific Coast	USA	Annual Grassland	36.20	-121.55	750	702	Obs.	30	2007
55	Hopland REC	North America	Pacific Coast	USA	Annual Grassland	39.01	-123.06	598	1127	Exp.	27	2007
56	Jasper Ridge Biological Preserve	North America	Pacific Coast	USA	Annual Grassland	37.41	-122.24	120	592	Obs.	30	2007
57	Leadbetter Point	North America	Pacific Coast	USA	Salt Marsh	46.61	-124.05	2	2072	Obs.	30	2007
58	Mclaughlin UCNRS	North America	Pacific Coast	USA	Annual Grassland	38.86	-122.41	642	867	Exp.	30	2007
59	Sedgwick Reserve UCNRS	North America	Pacific Coast	USA	Annual Grassland	34.70	-120.02	550	521	Obs.	30	2007
60	Sierra Foothills REC	North America	Pacific Coast	USA	Annual Grassland	39.24	-121.28	197	935	Exp.	30	2007
61	Smith Prairie	North America	Pacific Coast	USA	Mesic Grassland	48.21	-122.62	62	597	Exp.	30	2007
62	Mar Chiquita	South America	South America	Argentina	Mesic Grassland	-37.72	-57.42	6	838	Obs.	30	2011

Table A2. Final regression model of exotic cover and exotic richness at the site scale (N=62) explained by environmental covariates. Tests of significance are based on quasi-likelihood due to significant over- or under-dispersion in the data. Only the reduced model is shown. The full model included elevation (m); precipitation (mm yr^{-1}); seasonal precipitation and temperature variation; mean, maximum, and minimum annual temperature (C); aboveground live biomass (log g m^{-2} yr^{-1}); aboveground dead biomass (log g m^{-2}). Estimated dispersion parameter for quasi-likelihood was 0.56 for exotic cover, 4.24 for exotic richness, and 3.10 for native grass richness.

Response	Source	Estimate	Type II S.S.	D.F.	F	p
Exotic Cover	Mean Annual Temp.	0.227	8.03	1	14.3	0.000
	Temp. Wettest Quarter	-0.133	7.08	1	12.6	0.001
	Residuals		33.17	59		
Exotic Richness	Temp. Driest Quarter	0.065	51.78	1	12.2	0.001
	Residuals		254.36	60		
Native Grass Richness	Elevation	0.447	33.89	1	10.9	0.002
	Temp. Wettest Quarter	0.040	34.95	1	11.3	0.001
	Residuals		179.78	58		

Table A3. Author contributions to manuscript.

Full Name	Wrote the paper, e.g. contributed substantially to at least one section of the paper	Analyzed data, e.g. generated models (statisical and/or mathematical), figures, tables, maps, diagrams etc.	Developed and framed research questions for specific study using Nutrient Network data	Nutrient Network coordinators, e.g. designed experiments, coordinates network data collection and compilation, and garners funding.	Contributed substantially to data analyses, e.g. provided comments and suggestions	Contributed to paper writing, e.g. provided comments and suggestions	Collected Data
Eric Seabloom	X	X	X	X	X	X	X
Elizabeth Borer			X	X	X	X	X
Yvonne Buckley					X	X	X
Elsa Cleland			X		X	X	X
Kendi Davies					X	X	X
Jennifer Firn			X		X	X	X
W. Stanley Harpole			X	X	X	X	X
Yann Hautier					X	X	X
Eric M. Lind				X	X	X	X
Andrew MacDougall			X		X	X	X
John L. Orrock					X	X	X
Suzanne M Prober					X	X	X
Peter Adler						X	X
Juan Alberti							X
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Maria Caldeira							X
Chengjin Chu							X
Michael J. Crawley					X		X
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Andy Hector						X	X
Aveliina Helm							X
Helmut Hillebrand							X
Kirsten S. Hofmockel						X	X
Hope C. Humphries							X
Oscar Iribarne							X
Virginia L. Jin							X
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Johannes M. H. Knops						X	X
Kimberly J. La Pierre						X	X
Laura M. Ladwig							X
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Andrew DB Leakey						X	X
Qi Li							X
Wei Li							X
Rebecca McCulley						X	X
Brett Melbourne							X
Charles Mitchell						X	X
Joslin L. Moore						X	X
John Morgan						X	X
Brent Mortensen						X	X
Lydia R. O'Halloran				X			X
Meelis Pärtel						X	X
Jesús Pascual							X
David Pyke						X	X
Anita C. Risch						X	X
Roberto Salguero-Gómez						X	X
Mahesh Sankaran							X
Martin Schuetz						X	X
Anna Simonsen							X
Melinda Smith							X
Carly Stevens						X	X
Lauren Sullivan						X	X
Glenda M. Wardle							X
Elizabeth M. Wolkovich						X	X
Peter D. Wragg						X	X
Justin Wright							X
Louie Yang						X	X